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Wood and bark anatomy of *Hypocalyptus* support its isolated taxonomic position in Leguminosae

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ABSTRACT

The wood and bark anatomy of all three species of *Hypocalyptus* from the monotypic South African endemic tribe Hypocalypteae were studied. Despite large morphological differences (especially in habit) the species were found to be similar in wood and bark structure. Discontinuities are quantitative only, relating mainly to differences in growth form between *H. oxalidifolius*, a short-lived shrublet, and the two other species, *H. coluteoides* and *H. sophoroides*, both of which are erect shrubs or small trees of up to 6 m tall. *Hypocalyptus* wood has a mesomorphic structure with vessels solitary or in small groups, reflecting relatively moist habitats in fynbos vegetation. In contrast to many genera of Leguminosae for which data are available, crystals are absent from the wood. This is the first report of tanniniferous tubes in the wood of Leguminosae (previously reported only in Myristicaceae and a genus from Ulmaceae). The presence of tanniniferous tubes and the absence of crystals in all three species of *Hypocalyptus* underline the isolated position of the genus and support its tribal status.

1. Introduction

Hypocalyptus Thunb. is a South-African, fynbos-endemic genus comprising three species: *Hypocalyptus coluteoides* (Lam.) R.Dahlgren, *Hypocalyptus oxalidifolius* (Sims) E.Phillips and *Hypocalyptus sophoroides* Druce. All *Hypocalyptus* species occur only in the winter rainfall area of the Cape Floristic Region and grow in fynbos vegetation. *H. sophoroides* and *H. coluteoides* are shrubs or small trees of up to 6 m high, while *H. oxalidifolius* is a low sprawling shrublet up to 0.3 m high and up to 0.6 m wide (Dahlgren, 1972; Goldblatt and Manning, 2000). The three species grow on relatively moist sandstone slopes and beside streams.

Phylogenetic relationships of the genus have been unclear and its tribal position has been changed a number of times in the last few decades. Polhill (1981) included the genus in the tribe Liparieae, while Yakovlev (1991) placed *Hypocalyptus* as a separate subtribe within the tribe Liparieae. Detailed morphological, chemical and embryological studies by Van Wyk and Schutte (1995) and Schutte and Van Wyk (1998a) resulted in the exclusion of *Hypocalyptus* from the genistoid tribes. The unique combination of characters showed that the genus should be separated as a monotypic tribe (Schutte and Van Wyk, 1998a). Molecular systematic studies (Crisp et al., 2000; Wojciechowski et al., 2004) confirmed that the Hypocalypteae is related to the Australian tribes Mirbelieae and Bossiaeeae (Van Wyk, 2005 and references therein). In sister group relation to that alliance is the clade which includes the tribe Indigofereae, several tribes of the Milettioid group, a few tribes of the Phaseoleoid group and the large Hologalegina group. All these clades, together with the Baphioid clade of Sophoreae in the basal position, form the so-called Old World clade of Papilionoideae (Lewis et al., 2005).

Although the wood anatomy of the Leguminosae is relatively well known (Gasson, 1994; Lavin et al., 2001; Gasson et al., 2004; etc.), the majority of tribes of Papilionoideae remain to be studied. It has been suggested that wood anatomical characters are useful in studying relationships at tribal and generic levels in Leguminosae (Gasson, 2001). Bark structure is less often studied but proved to have systematic value in some families that have been investigated, such as Annonaceae (Junikka and Koek-Noorman, 2007), Araliaceae (Kotina and Oskolski, 2010), Rosaceae (Lotova and Timonin, 2005) and Salicaceae (Eremin and Shkuratova, 2007). In Leguminosae, available evidence is widely scattered in the literature and is often incomplete. A recent example of the taxonomic value of bark characters is the study of Boatwright et al. (2009), where the rate of periderm formation was used as the main diagnostic character to distinguish between various segregate genera of *Lebeckia* Thunb. sensu lato. The only available information on the wood and bark anatomy of *Hypocalyptus* is some notes in Metcalfe and Chalk (1950). Our work was aimed at generating new comparative data for this enigmatic genus and to contribute towards a better understanding of its tribal position and phylogenetic relationships.

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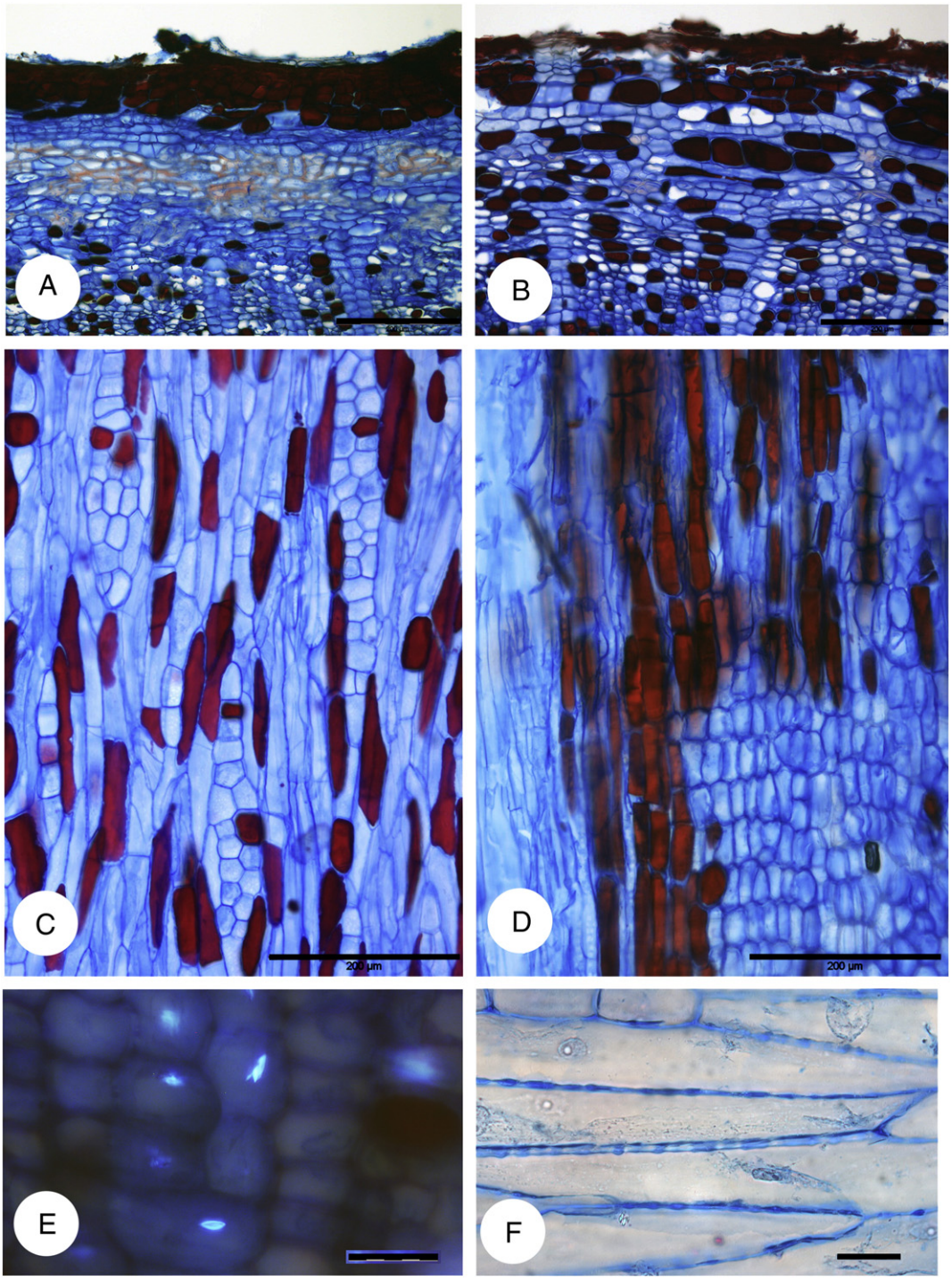

Fig. 1. Bark anatomy of *Hypocalyptus*. LM. (A, B) Dilated cortex and secondary phloem, and distribution of tanniferous cells, TS: (A) Sclerification of parenchyma cells in dilated cortex of *H. sophoroides*, TS; (B) Multicellular strands of parenchyma cells in dilated cortex of *H. oxalidifolius*, TS. (C, D) Distribution of tanniferous cells in secondary phloem: (C) Secondary phloem rays and axial parenchyma cells in *H. sophoroides*, TLS; (D) Upright cells in ray and strands of axial parenchyma cells of *H. coluteoides*, RLS; (E) Small navicular crystals in cortical parenchyma cells of *H. sophoroides*, TS; (F) Sieve tubes with compound sieve plates in *H. sophoroides*, TLS. Scale bars: 200 µm (A–D), 20 µm (E, F).

2. Materials and methods

Wood and bark samples, together with voucher specimens (all in JRAU) were collected in the Western Cape Province of South Africa. *H. oxalidifolius* was collected at Fernkloof Nature Reserve, Hermanus (Van Wyk and Kotina s.n.; preserved material labelled KK 07–10), *H. colutioides* at Storms River, Tsitsikamma (Van Wyk et al., s.n.; KK 42–11) and *H. sophoroides* at Du Toit's Kloof (Van Wyk 3012; KK 62–11). For investigation of bark anatomy, three pieces of stem (≈20–100 mm long) of different ages were collected from (1) branch tips without a visible periderm layer; (2) lower parts of the stem where the periderm was starting to develop; (3) thick stems with mature bark; and the last parts were also used for the wood anatomical study. Material was fixed in the standard mixture of formalin, acetic acid and alcohol (FAA; Johansen, 1940). Transverse, radial and tangential sections of bark (of different ages) and wood were made on a freezing and rotary microtome (Ernst Leitz GMBH, Wetzlar, Germany and Jung AG Heidelberg, Germany) and then stained with a mixture of

Table 1
Quantitative characters of the wood and bark of *Hypocalyptus*.

	H. coluteoides KK 42–11	*H. oxalidifolius* KK 07–10	*H. sophoroides* KK 62–11
Diameter of shoot, mm	12	6	9
Length of vessel elements, (mean ± error, min–max, μm)	257 ± 10	191 ± 7	228 ± 10
	148–368	121–260	119–316
Length of wood fibres,	654 ± 24	704 ± 21	760 ± 19
(mean ± error, min–max, μm)	375–1023	505–963	526–964
Number of vessel lumina per mm^2 (mean, min–max)	26	115	47
	24–28	89–141	44–53
Mean number of vessel lumina per group	1.4	1.9	1.4
Percent of solitary vessels	54	28	54
Fibre wall thickness	1.5–2.5	3–4.5	1.5–3.5
(min–max, μm)			
Vessel wall thickness	2,5–5	3–6	2–4
(min–max, μm)			
Tangential diameter of vessels, (mean ± error, min–max, μm)	47 ± 1.9	36 ± 2.0	38 ± 2.2
	25–50	14–52	20–69
Width of multiseriate rays in wood,	40.7 ± 1.5	41.7 ± 1.7	38 ± 1.4
(mean ± error, min–max, μm)	27–60	25–62	20–56
Height of multiseriate rays in wood,	353 ± 20	381 ± 29	439 ± 43
(mean ± error, min–max, μm)	177–635	131–788	126–897
Number of rays per mm in wood (mean ± error, min–max)	5.5 ± 0.3	8.7 ± 0.4	8 ± 0.4
	4–7	6–11	7–11
Vertical diameter of intervessel pits (min–max, μm)	2–5	3–5	3–5
Horizontal diameter of intervessel pits (min–max, μm)	4–11	5–10	4–10
Length of sieve tubes	305 ± 7	214 ± 5	187 ± 5
(mean ± error, min–max, μm)	234–385	156–286	115–243
Diameter of sieve tubes	18 ± 0.8	18 ± 0.9	18 ± 0.7
(mean ± error, min–max, μm)	13–21	14–21	15–22
Length of phloem fibres	1278 ± 66	770 ± 34	1214 ± 35
(mean ± error, min–max, μm)	1052–1634	492–942	928–1619
Width of multiseriate rays in phloem (mean ± error, min–max, μm)	55 ± 2.3	54 ± 2.7	55 ± 2.5
	33–77	30–84	28–88
Height of multiseriate rays in phloem (mean ± error, min–max, μm)	397 ± 24	279 ± 22	359 ± 24
	212–783	146–544	138–620
Number of rays per mm in phloem (mean ± error, min–max)	5.8 ± 0.2	4.7 ± 0.4	6.0 ± 0.4
	5–7	3–6	5–9

alcian blue and safranin (Jansen et al., 2004). Sections were mounted in Euparal. Maceration of wood and secondary phloem was carried out in Jeffrey's solution (Johansen, 1940). Measurements and photographs were made with an Olympus ColorView Soft Imaging System and Olympus Analysis Imaging Solutions (OASIS) programme. The descriptive terminology for bark follows those of Trockenbrodt (1990) and Junikka (1994). The descriptive terminology for wood follows that of the IAWA Committee (1989). The chemical test for tannins with $FeCl_3$ was made in accordance with Zhong et al. (1992). Two-year-old shoots from five species of three genera of Mirbellieae (*Daviesia corymbosa* Sm., *Daviesia leptophylla* A.Cunn. ex Don, *Dillwynia parvifolia* R.Br., *Dillwynia sericea* A.Cunn., and *Pultenaea subspicata* Benth.) and one species of Bossiaeeae (*Bossiaea eriocarpa* Benth.) were used in a preliminary study to check for the possible occurrence of tanniniferous tubes in the wood.

3. Results

3.1. Bark anatomy

The surface of young stems is smooth, reddish, and covered by a prominent indumentum. The epidermis on young parts of the stems is composed of a single layer of dome-like to isodiametric thin-walled cells with simple uniseriate trichomes of one or two short basal cells and an elongated terminal cell. The epidermis persists for a few years in all the studied species. With increasing diameter of the stem, the epidermal cells become stretched and divide anticlinally, thus forming strands of two or four cells. The average thickness of the cuticle in *H. oxalidifolius* is 9.6 μm, whereas that of both the other species is 2.4–3.0 μm. The cortex is composed of 4 to 10 layers of isodiametric to somewhat radially-flattened, thin-walled parenchyma cells, 10–30 μm in tangential diameter, containing chloroplasts or tannins (tanniniferous cells can be as much as 60 μm in diameter). Cells with tannins are concentrated near the external surface (Fig. 1A, B). Dilatation of the cortical tissue is effected mostly by tangential stretching of cells and also by the anticlinal division of the cortical parenchyma cells, thus forming strands of two to six cells (Fig. 1B). The cells of the dilated cortex contain starch grains. Sclerification of parenchyma cells occurs in the dilated cortex of only *H. sophoroides* (Fig. 1A). Small navicular crystals are occasionally present in the cortical parenchyma cells of all studied species (Fig. 1E). These crystals are either solitary or in aggregates. Primary phloem fibres have sclerified walls and occur in tangentially-stretched groups of 3 to 20 cells in *H. oxalidifolius* and in larger numbers (up to 100) in the other species. These groups may be arranged into a nearly continuous ring, of two up to six cells in width, being interrupted only by medullary rays.

The surface of the mature bark is brownish with shallow-fissured and light-coloured lenticels. The initiation of the first-formed periderm is subepidermal. The phellem is composed of two to five (up to 10 in *H. coluteoides*) layers of radially-flattened thin-walled cells containing tannins. The phelloderm comprises two to five layers of radially-flattened cells with tannins and starch grains. The first-formed periderm persists for many years in all studied species. Subsequent periderms are formed in deeper layers of the bark as a ring or as elongated scales which cut off thin layers of the collapsed tissues. The secondary phloem is composed of tangential zones comprising sieve elements and companion cells which alternate with axial parenchyma cells and are permeated by a network of phloem rays. Sieve tubes are 14–22 μm wide, with sieve tube members having a length that varies between 115–385 μm. Sieve plates are compound (Fig. 1F) and located on oblique cross walls (with 2 to 10 sieve areas) and also on the lateral walls (sometimes along the entire

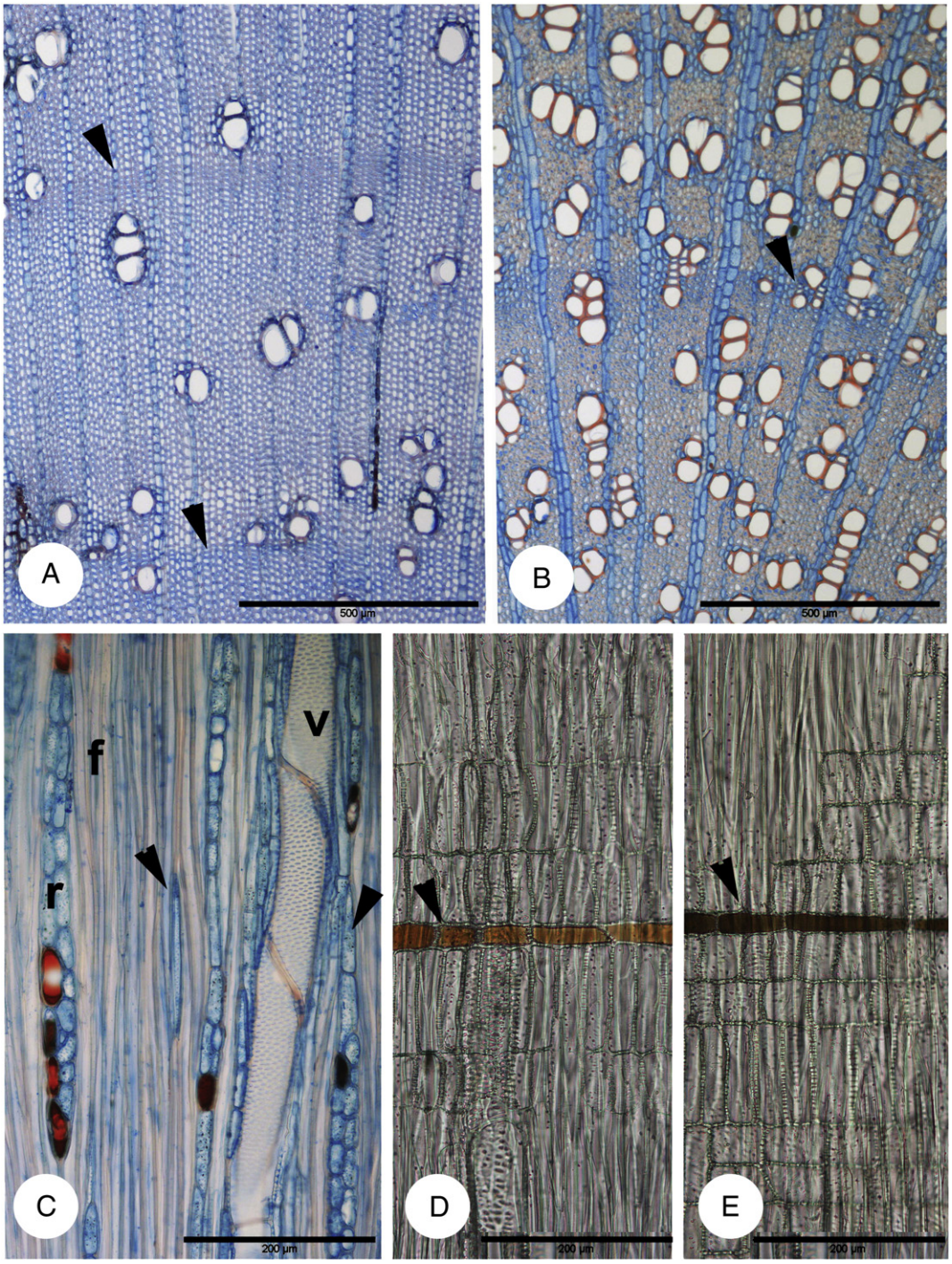

Fig. 2. Wood anatomy of *Hypocalyptus*. (A) *H. coluteoides*, TS. Arrows show growth ring boundaries; (B) *H. oxalidifolius*, TS. Arrow indicates growth ring boundary; (C) *H. sophoroides*, TLS. r — ray, v — vessel, f — fibre, arrows show axial parenchyma; (D) *H. sophoroides*: tanniniferous tube (arrow), natural colour, RLS; (E) *H. sophoroides*: tanniniferous tube (arrow), after reaction with FeCl3, RLS. Scale bars: 500 µm (A, B), 200 µm (C–E).

length of the cell). Axial parenchyma cells are fusiform and in strands of two to six cells (up to eight in *H. oxalidifolius*). The transition from non-collapsed to collapsed secondary phloem is gradual. Axial parenchyma cells in collapsed secondary phloem occur as thin-walled strands with tannins (Fig. 1C, D) and, rarely, small navicular crystals, strands of sclerified cells and fibres (Table 1). Secondary phloem rays are 1–3(4)-seriate and composed of procumbent, square and upright cells (Fig. 1C, D). Rays cells often contain tannins and sometimes small navicular crystals (Fig. 1E).

Dilatation of secondary phloem is radial. Dilated rays are extensively enlarged, mostly by tangential expansion and also by anticlinal divisions of ray cells resulting in rays of up to 10 cells wide.

3.2. Wood anatomy

Growth rings are absent (*H. sophoroides* KK 62–11) or distinct to faint, and marked by rows of weakly flattened fibres (*H. coluteoides*, *H. sophoroides* BEVW 3012; Fig. 2A) or differences in vessel diameter

(*H. oxalidifolius*; Fig. 2B). Wood is diffuse-porous. Vessels are solitary and in radial and oblique multiples of 2 to 4 cells and small clusters. Perforation plates are simple and intervessel pits alternate (Fig. 2C), round and oval to polygonal, with vestured narrow, oval apertures. Vessel-parenchyma pits are similar to the intervessel pits in shape and size. Fibres are non-septate (Fig. 2C), thin- to thick-walled (Fig. 2B), being very thin-walled in both specimens of *H. sophoroides*, often gelatinous, with minute simple pits, and more common on radial than tangential walls. Axial parenchyma is scarce paratracheal and vasicentric, also in narrow bands in *H. sophoroides*, fusiform and in two to four cells per strand. Rays are 1–3-seriate, composed of procumbent, upright and square cells. Crystals were not found. Tanniniferous tubes and cells occur in the rays, and the latter in the axial parenchyma strands (Fig. 2C, D, E). In contrast, no tanniniferous tubes were found in the five wood samples of the tribe Mirbelieae and one sample of the tribe Bossiaeeae.

4. Discussion

H. oxalidifolius is markedly different from the other two species, not only in the small, shrubby habit but also in the shape and size of the leaves, flowers and fruits. It is therefore noteworthy that the wood and bark anatomy are similar in all the species and specimens studied. Differences between species are quantitative only and can be related to differences in habit and the size of the plants. *H. oxalidifolius* has a thicker cuticle, shorter vessel elements, more numerous and larger groups of vessels, thicker-walled wood fibres, and shorter and less numerous rays in the bark. These characters may be influenced by environmental conditions — the thickness of the cuticle, for example, can be affected by solar radiation, temperature and water stress (Skoss, 1955).

As in the majority of Leguminosae, all species of *Hypocalyptus* have diffuse-porous wood, simple perforation plates, alternate-vestured intervessel pits and vessel-ray pits of similar size (Gasson, 1994). The wood of *Hypocalyptus* species is relatively mesomorphic in structure because of the presence of solitary vessels or vessels in small groups. In contrast, most genera of the tribe Podalyrieae (including the Liparieae, where *Hypocalyptus* was once placed) have strongly grouped vessels, often in a dendritic pattern (Van Wyk and Schutte, 1995). It is known that a dendritic pattern in Leguminosae is frequently associated with helical thickenings (Gasson, 1994). The mesomorphic structure of wood is commonly found in the tropical taxa of the Old World clade of legumes but unusual for taxa in a Mediterranean climate with severe summer aridity. In the latter, the wood is often xeromorphic, so that the wood structure of *Hypocalyptus* species may be restricting their distribution in fynbos to relatively localised and moist habitats. Data about the wood structure of fynbos plants are rare, but it seems reasonable to suppose that they commonly have some adaptation to water stress (Jacobsen et al., 2007). Surprisingly, the wood of some fynbos-endemic families such as Geissolomataceae, Roridulaceae, Bruniaceae, Stilbaceae and Retziaceae (Carlquist, 1975, 1976, 1978, 1986) have scalariform perforation plates, a character rarely found in plants of water-stressed habitats. Most of the species from these families appear to be adapted to water stress in having very narrow and highly grouped vessels (Carlquist, 1978, 1986). Another notable character, absent in *Hypocalyptus* but present in most of the woody Papilionoideae is the storied arrangement of wood elements.

Further evidence that *Hypocalyptus* was misplaced amongst the Cape genistoid legumes (mainly Podalyrieae, which now includes Liparieae) comes from bark anatomy. While in *Hypocalyptus* sieve areas are compound and occur on the lateral walls, those of *Virgilia* and other Cape genistoids are simple and placed on transverse walls (Stepanova et al., 2013-this issue).

The absence of crystals in the wood of *Hypocalyptus* is noteworthy, as crystals commonly occur in the wood of many Leguminosae (Gasson, 1994) including the tribe Podalyrieae, with which it co-occurs as fynbos-endemic taxa. *Hypocalyptus* also differs from several genera and species of the tribes of the Old World clade with which the genus is currently placed (Crisp et al., 2000; Wojciechowski et al., 2004; Van Wyk, 2005). Most of the taxa for which data are available have crystals in their wood. These include the tribe Indigofereae (information from Insidewood database: InsideWood, 2004-onwards), Millettieae (Gasson et al., 2004), Phaseoleae (Insidewood), Desmodieae (Insidewood), Robinieae (Insidewood) and the Baphioid group (Den Outer and Van Veenendaal, 1992). However, crystals were noted neither in *Notospartium carmichaeliae* Hook.f. (IRLC-Millettioids-clade) nor *Caragana frutex* (L.) K.Koch (tribe Hedysareae, in both cases of information from Insidewood database). In the tribe Galegeae, the absence of calcium oxalate crystals is suggested to be a unique character amongst papilionoid tribes (Lersten and Horner, 2007).

The most important discovery made in this study is the presence of tanniniferous tubes in the wood of *Hypocalyptus* (visible even in one-year old wood). Tanniniferous cells are widespread in Leguminosae and other families but tanniniferous tubes are very rare. These tannin-containing structures are longer than normal ray cells. They are known to be a common and specific character for Myristicaceae (Siddiqi and Wilson, 1974; Armstrong and Wilson, 1980; Garratt, 1993) and were later also observed in *Pteroceltis* Maxim. of the Ulmaceae (Zhong et al., 1992). Thus the presence of tanniniferous tubes in *Hypocalyptus* is only the third record for dicotyledonous woods. Unfortunately, anatomists rarely do chemical analyses of cellular substances, but at least a brown content in some stem cells has been found in most subclades of the Old World clade, except the three monotypic tribes Sesbanieae, Cicereae and Abreae, the tribe Trifolieae and the Baphioid group (Metcalfe and Chalk, 1950). We could not find any published wood anatomical descriptions for the Bossiaeeae and Mirbelieae, and no reference to tannins in these tribes, which are regarded as possible sister groups of the tribe Hypocalypteae. Although a brown cellular content is described for many Leguminosae, including species from groups closely related to *Hypocalyptus*, tanniniferous tubes have not yet been reported for the family. The absence of tanniniferous tubes in two-year old wood from the limited samples of the tribes Mirbelieae and Bossiaeeae that we were able to study, strongly supports the isolated position of genus in the family and is in agreement with its tribal status (Schutte and Van Wyk, 1998a,b). The analysis of the wood structure in these clades can be useful for unravelling their intergeneric relationships which are still unclear (Ross and Crisp, 2005) and is necessary for understanding the evolution of wood characters in all of the Old World clades.

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